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TEMPORAL VARIATION OF MORPHOLOGICAL DISPARITY IN THE SYNAPSIDA[1]

(With 3 figures)

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ABSTRACT: Patterns of temporal variation of morphological disparity along 100 million years of synapsid evolution were analyzed with quantitative methods. Morphological disparity along four stratigraphic intervals (from Middle Carboniferous to Upper Triassic) was quantified by the maximum and mean pairwise dissimilarity among taxa and by the range and total variance of morphospace occupied. The greatest morphological disparity occurred in the Upper Permian, with an accentuated decline during the Permo-Triassic Crisis followed by another increase in the Middle and Upper Triassic, suggesting the existence of effective limits to the potential morphospace that could be explored during the evolution of this group.

Key words: morphological diversity, morphospaces, multivariate analysis, mammal-like reptiles, mass extinction.

RESUMO: Variação temporal da disparidade morfológica em Synapsida.

Os padrões de variação temporal da disparidade morfológica ao longo de 110 ma de evolução dos Synapsida foram analisados com métodos quantitativos. A disparidade morfológica ao longo de quatro intervalos estratigráficos (do Carbonífero Médio ao Triássico Superior) foi quantificada pelas distâncias máxima e média entre os táxons e pela amplitude e variância total do morfoespaço ocupado. A maior disparidade morfológica ocorreu no Permiano Superior, verificando-se um acentuado declínio da mesma durante a Crise Permo-Triássica e um novo aumento a partir do Triássico Médio e Superior, sugerindo a existência de limites efetivos ao morfoespaço potencial que pode ser explorado ao longo da evolução deste grupo.

Palavras-chave: diversidade morfológica, morfoespaços, análise multivariada, répteis mamaliformes, extinção em massa.

INTRODUCTION

The Synapsida or "mammal-like reptiles" were the dominant land vertebrates during the Permian and much of the Triassic, constituting a diverse and abundant group that later gave rise to the mammals.

Synapsid evolution spans an interval of 120 million years (from Carboniferous to Triassic) and has been characterized by three extensive adaptive radiations, each of which occurred after an extinction event that caused the disappearance of many of the lineages from the previous radiation (KEMP, 1982). During the Permo-Triassic Crisis a large fraction of synapsid families went extinct (ERWIN, 1994). A recent phylogenetic analysis of this group (SIDOR & HOPSON, 1998) suggested that rapid accumulation of derived characters was relatively infrequent in the synapsid lineage that gave rise to mammals, and that a gradual pattern of morphological change predominated during the evolution of this group.

The quantitative analysis of morphological diversity ("disparity" *sensu* GOULD, 1989) has attracted much interest in recent years (FOOTE, 1997). The use of numerical methods to analyze the occupation of multivariate spaces defined quantitatively ("morphospaces") makes possible the objective and precise description, interpretation, and comparison of patterns of morphological variation in a group of organisms, frequently allowing clarification of the evolutionary processes responsible for such patterns (GOULD, 1991). This approach is promising in the study of important paleobiological questions posed by the accumulation of data from the fossil record (JABLONSKI, 1999) and can, for example, contribute to a better understanding of the processes of survival and recovery following the great mass extinctions (ERWIN, 1998). Quantitative methods have been successfully applied to the investigation of patterns of morphological disparity in Paleozoic blastoids

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and trilobites (FOOTE, 1992, 1993) and Ordovician-Devonian crinoids (FOOTE, 1994, 1995), as well as to the comparison of anatomical designs in Cambrian and Recent arthropods and priapulids (WILLS, BRIGGS & FORTEY, 1994; WILLS, 1998).

However, there are no records in the paleontological literature of applications of this approach to the study of fossil vertebrates. The Synapsida offer an interesting opportunity to test the application of quantitative methods in the analysis of morphological disparity in a group of fossil vertebrates and investigate the effects of a mass extinction (in this case, the Permo-Triassic Crisis) on the evolution of the synapsid morphology.

MATERIAL AND METHODS

Data for this study as provided by SIDOR & HOPSON (1998). It consists of a matrix of 21 synapsid taxa and 181 qualitative multistate morphological characters (101 cranial, 21 dental, and 59 postcranial). The list of taxa and time scale used in this study are given in table 1.

This data matrix was used to obtain Manhattan distance matrices (SNEATH & SOKAL, 1973) among taxa. These matrices were computed for the full character set and for each individual set of characters, along four stratigraphic intervals (Middle Pennsylvanian, Late Permian, Middle Triassic, and Late Triassic), chosen to reflect a compromise between resolution and sample size

TABLE 1

Synapsid taxa and time scale used in this study

Number	Taxon	Period/Epoch	Stage/Sub-stage	FAD (ma)
1	Ophiacodontidae	Middle Pennsylvanian	Moscovian	310
2	Edaphosauridae	Late Pennsylvanian	Gzelian (Stephanian)	300
3	*Haptodus*	Late Pennsylvanian	Gzelian (Stephanian)	300
4	Sphenacodontidae	Late Pennsylvanian	Gzelian (Stephanian)	300
5	Biarmosuchia	Late Permian	Lower Kazanian	270
6	*Eotitanosuchus*	Late Permian	Lower Kazanian	270
7	Anteosauridae	Late Permian	Lower Kazanian	270
8	Estemmenosuchidae	Late Permian	Lower Kazanian	270
9	Anomodontia	Late Permian	Lower Kazanian	270
10	Gorgonopsidae	Late Permian	Upper Kazanian	266
11	Therocephalia	Late Permian	Upper Kazanian	266
12	*Dvinia*	Late Permian	Upper Tatarian	255
13	*Procynosuchus*	Late Permian	Upper Tatarian	255
14	Galesauridae	Late Permian	Upper Tatarian	255
15	*Thrinaxodon*	Lower Triassic	Lowest Induan	250
16	Cynognathia	Middle Triassic	Lowest Anisian	240
17	*Probainognathus*	Middle Triassic	Ladinian or Anisian	234
18	*Probelesodon*	Middle Triassic	Ladinian or Anisian	234
19	Tritheledontidae	Late Triassic	Norian (?Upper)	214
20	Morganucondontidae	Late Triassic	Norian (?Upper)	214
21	*Sinoconodon*	Early Jurassic	Lower Sinemurian	200

(FAD) First Appearance Date, estimated in millions of years before present.

(FOOTE, 1994). Distance matrices were then subjected to a principal coordinate analysis (SNEATH & SOKAL, 1973), and a minimum-spanning tree was superimposed on the ordination results. Morphological disparity was quantified by the maximum and average distance (dissimilarity) among taxa and by the range and total variance of morphospace occupied (FOOTE, 1994, 1997; WILLS, BRIGGS & FORTEY, 1994).

All statistical analyses were performed on an IBM-PC microcomputer with a 100MHz Pentium™ processor. Distance matrices and principal coordinates were computed using the NTSYS-pc package (ROHLF, 1993). Morphological disparity indices were calculated with programs in the C language written by Rick Lupia (available at http://geosci.uchicago.edu/paleo/csource/) and adapted by the author for running on the PC under MS-DOS with the DJGPP 32-bit compiler.

RESULTS AND DISCUSSION

Six eigenvectors with associated eigenvalues greater than zero, comprising 99.9% of the total morphological variation, were extracted from the distance matrix among taxa, computed from the data matrix of all characters. The projection of the scores of individual taxa on the first two eigenvectors, responsible for 85.8% of the total variation (Fig.1), displayed a pattern of morphospace occupation essentially concordant with the model of synapsid gradual evolution suggested by the phylogenetic analysis of SIDOR & HOPSON (1998).

Temporal patterns of morphological disparity and taxonomic diversity in each interval, as estimated by several indices (Tab.2), were similar for the full character set and for each individual character set (Figs.2, 3). The greatest morphological disparity in the Synapsida occurred in the Upper Permian, with an

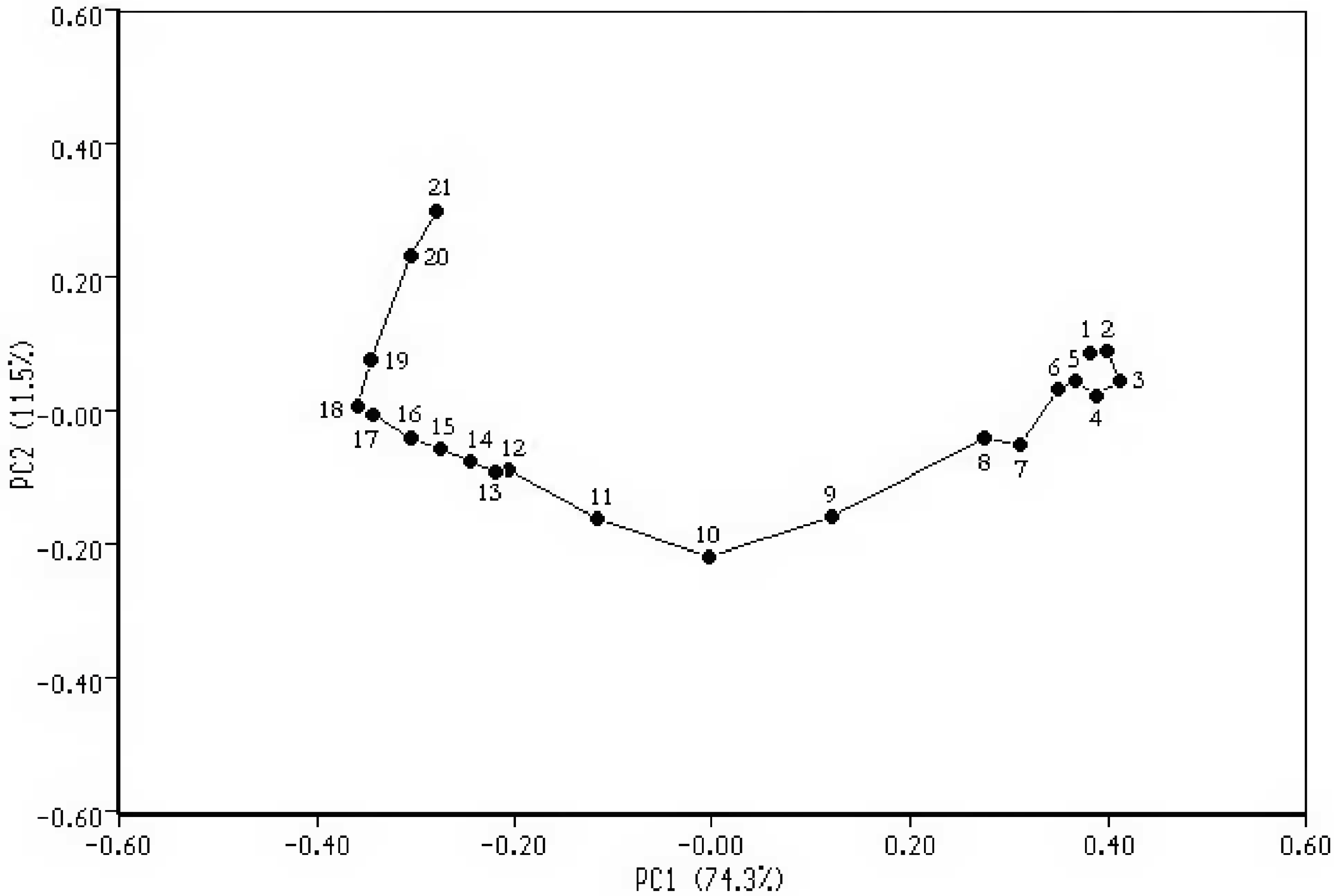

Fig.1- Projection of the scores of the synapsid taxa in the reduced space of first two principal-coordinate axes, with a minimum spanning tree superimposed upon the ordination (taxon numbers correspond to those of table 1).

TABLE 2

Morphological disparity and taxonomic diversity indices
for the Synapsida in the Carboniferous-Triassic interval

interval	taxonomic diversity	range	total variance	maximum distance	average distance
1	4	2.7465	0.1832	0.29299	0.19147
2	10	3.7243	0.0924	0.65409	0.37943
3	4	2.3499	0.1695	0.14724	0.09800
4	3	1.0027	0.0687	0.32692	0.28340

(1) Middle Pennsylvanian, (2) Late Permian, (3) Middle Triassic, (4) Late Triassic.

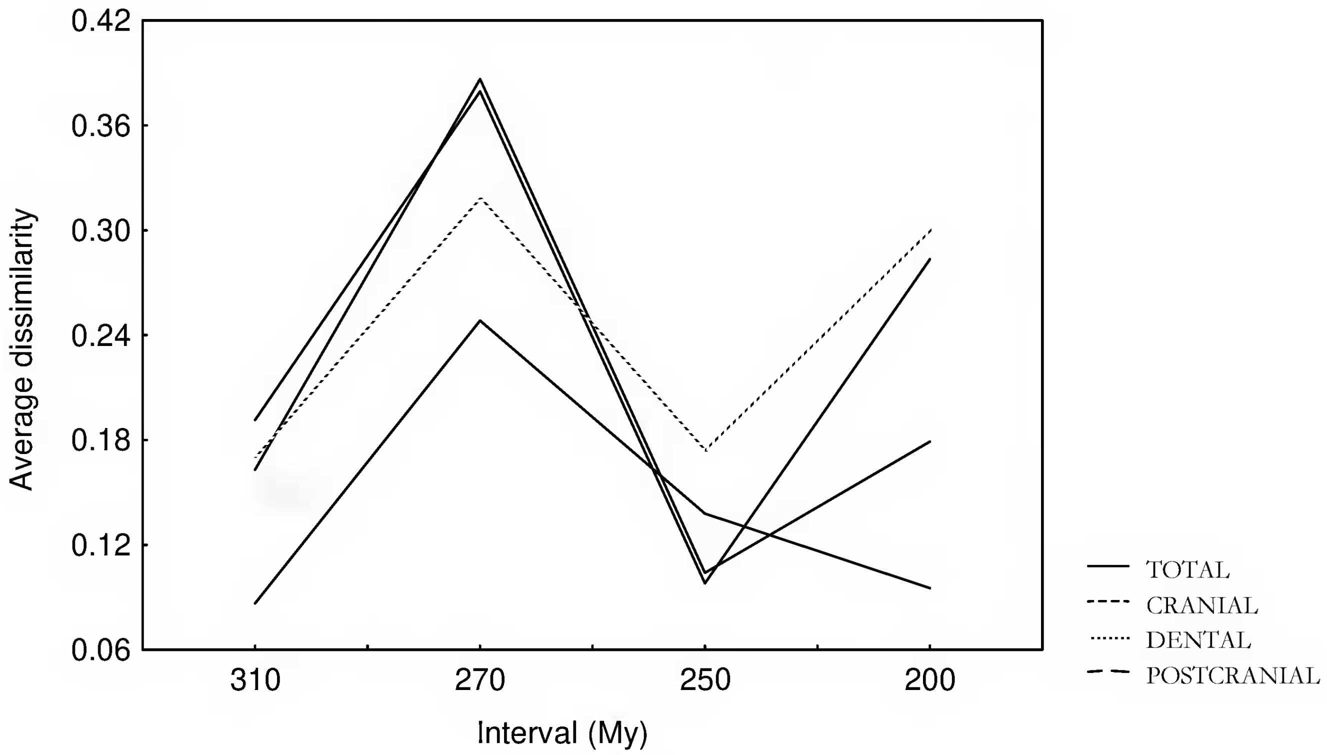

Fig.2- Temporal sequences of morphological disparity in the Synapsida based on the set of all characters and on each individual set of characters in the Carboniferous-Triassic interval, estimated by the mean pairwise dissimilarity between taxa.

accentuated decline during the Permo-Triassic Crisis followed by another increase in the Middle and Upper Triassic, reaching levels near those before the mass extinction. The diversity peaks before and after the Permo-Triassic Crisis seems therefore to have been reached at comparable rates.

The quantitative analysis of morphological disparity in the Synapsida suggests the existence of heterogeneities in certain regions of the morphospace, as those produced by increased extinction rates (FOOTE, 1993). Although synapsid evolution can be interpreted as a gradual process from a phylogenetic perspective, the quantitative analysis of morphological disparity in this group points out that the evolutionary patterns in the morphology of this group were not necessarily constant over time. In particular, the Permo-Triassic mass extinction had a pronounced effect on these patterns.

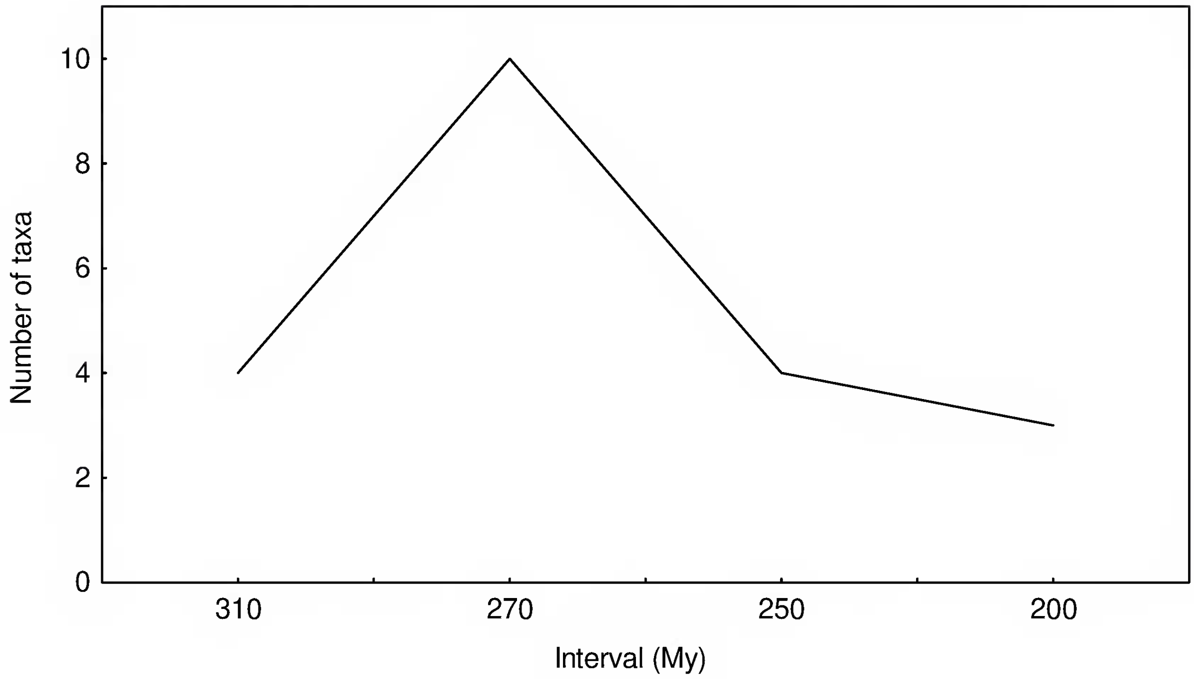

Fig.3- Temporal sequence of taxonomic diversity in the Synapsida in the Carboniferous-Triassic interval.

These results are consistent with those obtained in studies of morphological disparity in other groups (FOOTE, 1992, 1993, 1994, 1995, 1996; LUPIA, 1999), suggesting some degree of common control on diversification patterns in these groups in geological time (FOOTE, 1993). While the accelerated morphological diversification of the Synapsida after the mass extinctions in the end of the Paleozoic can imply that species belonging to individual higher taxa rapidly occupied the ecological spaces available in the beginning of the Mesozoic (FOOTE, 1996) they also provide some support for the notion of the existence of effective limits to the potential morphospace that can be explored during the evolution of a group (THOMAS & REIF, 1993; FOOTE, 1993).

A more detailed analysis, based on a larger number of synapsid taxa, is still needed in order to reach more definite conclusions. However, it seems clear that the quantitative analysis of morphological disparity constitute a potentially very promising approach to the study of evolutionary patterns in fossil vertebrate groups.

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